Science of the Total Environment 667 (2019) 16–24

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Modelling the effects of climate change on the distribution of benthic indicator species in the Eastern Mediterranean Sea

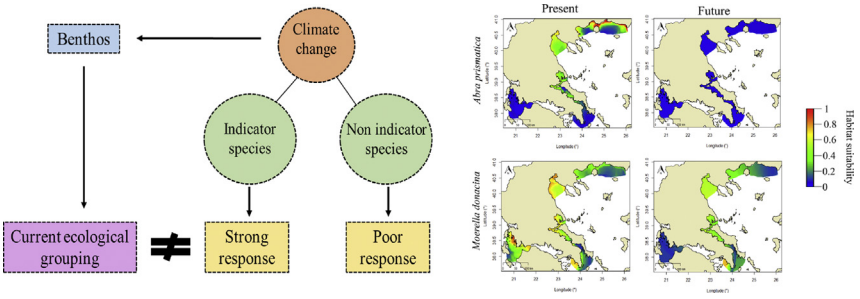
Manos L. Moraitis [a,*], Vasilis D. Valavanis [b], Ioannis Karakassis [a]

[a] Marine Ecology Laboratory, Department of Biology, University of Crete, PO Box 2208, GR 70013 Heraklion, Greece
[b] Hellenic Centre for Marine Research, Institute of Marine Biological Resources and Inland Waters, PO Box 2214, GR 71003, Heraklion, Greece

HIGHLIGHTS

- Climate change is expected to affect the distribution of benthic indicator species.
- The current ecological grouping is irrelevant under the scope of climate change.
- New perspective on the use of benthic species as biotic tools

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 7 December 2018
Received in revised form 18 February 2019
Accepted 21 February 2019
Available online 24 February 2019

Editor: Daniel Wunderlin

Keywords:
Benthos
Macrofauna
Climate change
Indicator species
Ecological groups
Species distribution modelling

ABSTRACT

The potential effects of climate change on the distribution of benthic species commonly used in marine ecological quality assessment were investigated using a spatial modelling approach. In this work, the relevance of the ecological groups that macrofaunal molluscs are assigned according to their sensitivity or tolerance to environmental disturbance was examined under the scope of the RCP 8.5 severe emissions scenario. The effects of climate change were more profound on species that are indicative of a specific suite of climatic conditions regarding temperature and salinity. Significant loss of habitat suitability was observed for the tolerant species *Corbula gibba* and *Abra prismatica* whereas the sensitive species *Moerella donacina* was least affected. In contrast, an overall expansion of the distributional potential was observed for the sensitive species *Flexopecten hyalinus* as newly suitable habitats are formed. As hypothesised, the current ecological grouping that depicts the sensitivity of a benthic species to an environmental stressor is irrelevant when assessing the effects of climate change. We propose a new standpoint of using benthic species as biotic tools based on their ecological niche requirements.

© 2019 Elsevier B.V. All rights reserved.

1. Introduction

The Mediterranean Sea is often described as a "hot spot" for climate change impacts (Giorgi, 2006) and it is expected to respond faster to this pressure than the open ocean counterparts due to a unique combination of hydrographic and geographical characteristics. More specifically, its location between two different climatic regimes (the arid climate of North Africa and the temperate climate of central Europe) and limited hydrological exchange with the open ocean, render the Mediterranean Sea more vulnerable to climatic alterations (Marbà et al., 2015). Recent studies conclude that the Mediterranean Sea will become warmer and more saline with varying consequences on the region's primary production in the immediate future (Macias et al., 2015; Piroddi et al., 2017). However, due to its semi-enclosed nature

Abbreviations: SDM, species distribution modelling.

* Corresponding author.
E-mail address: manomort@icloud.com (M.L. Moraitis).

https://doi.org/10.1016/j.scitotenv.2019.02.338
0048-9697/© 2019 Elsevier B.V. All rights reserved.

between two continents and its intricate orography, the Mediterranean Sea is characterized by regions of highly contrasting physical and chemical processes and the effects of climate change are expected to differ across the basin. The east-west and north-south environmental gradients are modulated even more by regional differences in areas with river outflow and complex topography (Basterretxea et al., 2018). One of the main challenges regarding the assessment of the effects of climate change in the Mediterranean region is the fact that not all areas are expected to be equally affected due to varying climatic conditions (Lejeusne et al., 2010). According to Spalding et al. (2007), the Mediterranean basin can be divided into further distinct provinces, two of which are the Aegean and the Ionian Seas. The Aegean Sea is characterized by strong hydrological fronts of temperature, salinity and primary productivity due to its geographic position between the Black Sea and the Ionian and Levantine Seas (Giannakourou et al., 2014). Additionally, the Ionian Sea is fronted by various water masses that depict a different hydrographic pattern to the nearby Aegean province (Menna and Poulain, 2009). Even though climate change impact on the Mediterranean marine biota has been documented (Lejeusne et al., 2010), there is a gap of knowledge on predicting the effects of climate change on the distribution of marine species in such dynamic areas.

Soft-bottom macrobenthic species have been traditionally used as biotic tools for assessing the ecological quality status of the Mediterranean benthic ecosystems and have been proven useful proxies for evaluating the impact of various pressures in coastal and transitional aquatic environments (Dauvin et al., 2017; de-la-Ossa-Carretero et al., 2012; Moraitis et al., 2013). Their relatively sessile nature is a main attribute that distinguishes macrofaunal species as environmental stress proxies because they are unable to avoid deteriorating environmental conditions (Sánchez-Moyano et al., 2017). Mollusca in particular is the most sedentary group and due to their significantly wider range of tolerance than the rest of macrofauna (Nerlović et al., 2011; Pearson and Rosenberg, 1978) are an ideal biotic tool for marine ecological status assessment (Moraitis et al., 2018). The most relevant benthic biotic indices used in aquatic health assessment assign macrobenthic species into different ecological groups according to their sensitivity or tolerance to a specific environmental stressor, mainly organic enrichment with consequent low redox potential and hypoxia (Borja et al., 2000; Dauvin and Ruellet, 2007; Rosenberg et al., 2004; Simboura and Zenetos, 2002). Therefore, it is expected that species of the same ecological group would respond with the same coping strategy in environmentally disturbed habitats. This assumption has been proven in cases regarding the impact of organic pollution (Dauvin and Ruellet, 2007). However, it is unclear if the aforementioned species grouping is evident under different climate change scenarios.

Species distribution models (SDMs) are essential tools for predicting the effects of climate change and marine global warming on species distributions. The incorporation of benthic molluscs in SDMs for assessing the effects of different climate change scenarios is focused mainly on biological invaders (Jones et al., 2013; Raybaud et al., 2014; Sarà et al., 2018), species of socioeconomic interest (Appelqvist et al., 2015; Russell et al., 2012) and of high ecological value (i.e. important role in ecosystem functioning) (Gormley et al., 2013) or a combination of the aforementioned categories (Saeedi et al., 2017; Saupe et al., 2014). To our knowledge, studies regarding the distribution of molluscan species under climate change in the Mediterranean region are scarce (Sarà et al., 2018) and not under the scope of re-examining the baselines of benthic ecology that have been traditionally used for marine health assessment.

The aims of this study were to: i) predict the potential impact of the extreme climate change scenario RCP 8.5 (worst-case scenario forecasting the continuous increase of greenhouse gas emissions) on the distribution of benthic molluscs commonly used in environmental impact assessment for the year 2100; ii) evaluate the relevance of their current ecological grouping according to the baselines of macrobenthic ecology in response to climate change; and iii) examine the features that mark the resistance or vulnerability of benthic species to climate change. We assume that species indicative of a specific suite of environmental conditions would respond to climate change according to their ecological preferences regardless of their current ecological grouping. Future climatic conditions are expected to greatly affect the distribution of these indicative species compared to others occupying a broader ecological niche. To our knowledge, no other study has addressed the potential impacts of climate change on the distribution of benthic organisms traditionally used in environmental disturbance assessment in the Mediterranean basin using relevant modelling methods.

2. Materials and methods

2.1. Study design

The purpose of this study's sampling design was to capture the main environmental gradients originating in the Aegean Sea (i.e. temperature, salinity, chl *a* concentration) in order to incorporate the full ecological response range of the benthic species that characterize this area. In order to be more coherent and avoid bias in the findings of this study, we also included sampling stations from the Ionian Sea (Fig. 1), a marine region characterized by stable environmental conditions. This design is based on Moraitis et al. (2018) and allows the full examination of the benthic species responses under a specific environmental issue (in this case climate change).

2.2. Biological data

In total, 123 soft-bottom macrofaunal samples were collected from the Aegean and Ionian Seas (Fig. 1). The sampling took place between April and July 2014, using a Smith-McIntyre grab with a sampling area of 0.1 m^2. After the collection, the macrofaunal samples were sieved first over a 1 mm and then a 0.5 mm mesh sieve and fixed with 10% formalin. Before transfer to the laboratory for further analyses, the samples were stained with Rose Bengal to facilitate sorting. In the laboratory, samples were sorted and identified to species level. All species names were checked for updates in their taxonomy through the World Register of Marine Species web page (WoRMS Editorial Board, 2018). For all species, additional information was compiled regarding their ecological grouping, defined using the BENTIX index classification list (Simboura and Zenetos, 2002). We have chosen to use this classification scheme because it has been designed and calibrated specifically for Greek waters.

In order to predict the current and future distribution of macrofaunal benthic assemblages under the effect of climate change, we incorporated molluscan species that are fundamentally used in marine health assessment in the Mediterranean Sea via the proposed benthic biotic index for the region (Simboura and Zenetos, 2002). The goal was to include species that are considered to be “tolerant” or “sensitive” to environmental disturbance and characterize environmentally disturbed and pristine ecosystems respectively. For this study we worked with *Corbula gibba* (Olivi, 1792) and *Abra prismatica* (Montagu, 1808) as tolerant species, and *Moerella donacina* (Linnaeus, 1758) and *Flexopecten hyalinus* (Poli, 1795) as sensitive species (Fig. S1). These species have been extensively used in environmental impact assessment and are incorporated as biotic tools in the aforementioned biotic index.

2.3. Climatic data

For the modelling procedure, only the most relevant environmental predictors for the study area were selected to predict the current and future distribution of the Aegean and Ionian benthic molluscs. Temperature, salinity and primary productivity are considered the most useful direct variables that should be incorporated in benthic SDMs (Reiss et al., 2015) and therefore were selected for this work. By incorporating biologically essential environmental predictors in the modelling process, the performance is enhanced and subsequently the overall model

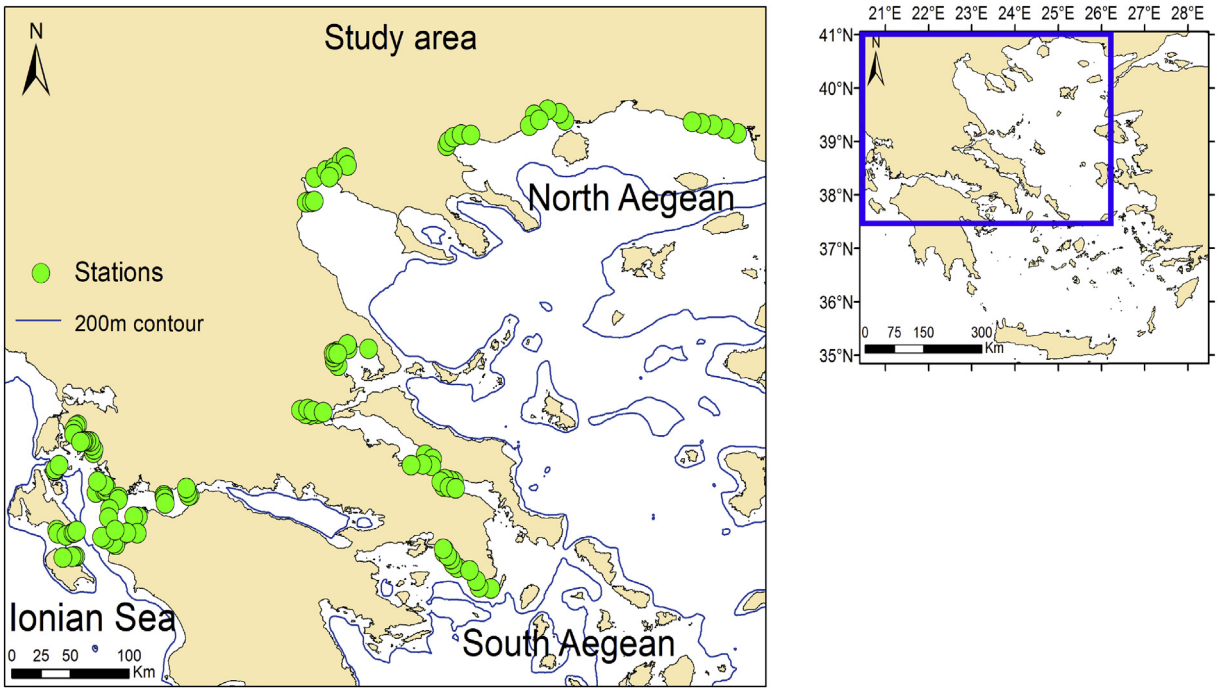


Fig. 1. Sampling stations located in the Aegean and Ionian Seas.

credibility increases (Kotta et al., 2014). Depth and substrate type are considered important components of the benthic ecosystem, however, they should be used with caution in benthic SDM studies; the former because it is plagued with collinearity issues with other environmental predictors (Reiss et al., 2015) and the latter because of the data unavailability in large spatial scales and extreme spatial variability at coarse resolution (Goldsmit et al., 2018; Saupe et al., 2014; Townhill et al., 2017). For the molluscan SDM in this study, sea surface and sea bottom predictors were initially tested for issues of collinearity. The collinearity diagnostic VIF (Variance Inflation Factor, cut-off threshold = 5), based on a stepwise process to identify and exclude collinear variables, and the Pearson correlation test (threshold > 0.5) were employed. All current and future marine layers were derived from Bio-Oracle, a global environmental dataset designed for marine species distribution modelling (http://www.bio-oracle.org/) (Tyberghein et al., 2012), which is comprised of satellite and in situ data. Future environmental grids for the year 2100 were based on the next generation RCP 8.5 (Representative Concentration Pathways - RCP). RCP 8.5 implies the continuous rising of radiative forcing pathway leading to 8.5 W/m^2 (~1370 ppm CO_2) by the year 2100 and predicts severe greenhouse gas emissions throughout the remainder of the century (van Vuuren et al., 2011). For the purpose of this work, all environmental layers were resampled by bilinear interpolation to a resolution of 1 km^2 according to previous studies in the area (Galanidi et al., 2016; Moraitis et al., 2018; Sarà et al., 2018). Further raster layer processing included cropping using a polygon mask to the extent of the sampling vicinity (i.e. depth up to 200 m). In order to ensure that all locations represent spatially unique measurements, we performed geographic filtering of the records at a fixed distanced buffer defined by the resolution of the environmental predictors using the spThin package (Aiello-Lammens et al., 2015). This practice is advised as a measure to mitigate sampling bias and spatial autocorrelation when evaluating environmental variables and improve model generalizability (Kramer-Schadt et al., 2013). All spatial and statistical analyses were conducted using the packages raster, rasterVis, usdm, maptools, maps and prettymapr in the R environment version 3.4.3 (R Development Core Team, 2018) and ArcGIS version 10.2. The final set of predictors consisted of sea-bottom temperature (Temperature – minimum), sea surface salinity (Salinity – mean) and surface chlorophyll *a* (Chl *a* - mean) concentration as a primary productivity measure (Figs. S2; S3). The selected environmental variables are ideal descriptors of the environmental variability of study area and have been previously used in molluscan SDM (Moraitis et al., 2018).

2.4. Ecological niche evaluation

In order to evaluate the relevance of the aforementioned sensitivity classes, we examined the ecological requirements that define the geographical limits of each species according to their present distributions. The evaluation of the species' ecological niche was achieved by quantifying the occupied environmental space of each species based on the ordination method proposed by Broennimann et al. (2012). In particular, a principal component analysis (PCA) was performed by calibrating the occupied environmental space of the study area based on the environmental layer pixel values. Additionally, a kernel density function was applied in order to smooth the density of each specie's records in each cell of the environmental grids. This approach mitigates sampling bias due to the dependency of the species occurrence records from the environmental data resolution and limits the effect of the environmental variability (Warren et al., 2008), which leads to an accurate manifestation of the suitability of the climatic conditions (Gama et al., 2017). Overestimation of the niche requirements was avoided due to the availability of true absences for each species, an issue that would otherwise have risen if random “background” absences were generated. The final outcome consists of the density of each species records plotted on the 100% and 50% of the available environmental space along the first two principal component axes. The analysis was conducted using the “ecospat” tool implemented in the R environment (Di Cola et al., 2017).

2.5. Modelling

Habitat suitability was estimated using the machine-learning algorithm MaxEnt (maximum entropy) version 3.4.1 (Phillips et al., 2006). This approach is ideal for projecting species' habitat suitability over temporal and spatial scales and has been regarded as the most effective method for projecting benthic molluscan distributions in future climate change scenarios (Saeedi et al., 2017; Sarà et al., 2018). Models are built

using the data splitting method of bootstrapping for 10 replicates in order to reduce uncertainty, and for each model run, 70% of the specie's records was randomly retained for training and 30% for testing. The background points number was set at 1000 in order to reduce modelling over-overfitting issues and the regularization multiplier was fixed at 1. The model performance was assessed according to the receiver-operating characteristic (ROC) curve (AUC) (Fielding and Bell, 1997), where values equal to 0.5 indicate random model performance and those above 0.7 good model performance. Environmental predictor importance was determined by the contribution of each predictor to the modelling performance in order to achieve the best fit during the training stage. In addition, permutation performance was also assessed by randomly permuting the values of each predictor on training presence and background data and measuring the variation of AUC value. Model transferability under the climate change scenario for the year 2100 was monitored with the "clamping" option (Elith et al., 2011). This method is used to identify areas of strict extrapolation (i.e. environmental predictor values outside the model training range) when projecting SDMs to different climatic conditions and mitigate this issue by constraining the pixel values of projected environment within the range of the training data.

The modelling output between the two climatic times (present and future) was compared in order to evaluate the vulnerability of each species under the extreme climate change scenario. Niche overlap between present and future distributions for each species was investigated using the Schoener's *D* distance indicator implemented in the ENMTools package (Warren et al., 2010). This indicator is considered ideal for computing niche overlaps from predicted species distributions generated from SDM models (Rödder and Engler, 2011). Schoener's *D* quantifies niche similarities with a value range of 0 (no overlap – different niches) to 1 (complete overlap – similar niches) (Warren et al., 2008). Niche overlap through different climatic times was assessed by using the difference between suitability scores at each grid cell after the standardisation of the habitat suitability maps so that all suitability scores of the grid cells add up to 1.

3. Results

3.1. Ecological niche

Ecological niche analysis suggested that *C. gibba* and *A. prismatica* occupy the same distinct areas of the first two principal climatic niche axes (density records) indicating similar ecological niche (Fig. 2). The analysis presented great variability in the environmental space inhabited by *M. donacina* and *F. hyalinus*, with the former occupying almost all the available environmental space and the latter showing one distinct area, inferring a strict preference for environmental conditions. PCA on climatic data showed that the first two components explained 97.27% of the data variation. Temperature contributed the most to the first axis loadings (−0.96) followed by salinity (−0.89) and chl *a* (0.71), accounting for 74.89% of the climatic conditions of the study area whereas the 22.38% variance explained by the second axis was attributed mainly to chl *a* (0.7) and salinity (0.39). *Corbula gibba* and *A. prismatica* occupy areas characterized by low temperatures, low salinity and increased chl *a* concentration whereas *F. hyalinus* is more abundant in areas with increased temperatures and salinity but with low chl *a* concentration. The results for *M. donacina* suggest that this species could inhabit a broad range of climatic conditions.

3.2. Modelling

All SDMs performed well for both present and future projections, with the AUC criterion value well above the defined threshold (AUC > 0.7) (Table 1). Overall, the habitat suitability of *C. gibba*, *A. prismatica* and *M. donacina* is expected to decline with increasing temperatures under the predicted future climatic conditions by 2100 (Fig. 3). Temperature and salinity were the most important environmental predictors for the species' distributions in this study (Table 1). *Corbula gibba* and *A. prismatica* are more vulnerable to temperature increase than *M. donacina* for which this factor had less influence than salinity and chl *a* concentration (Fig. S4). Unlike the other species of this study, SDM rendered increased habitat suitability for *F. hyalinus* driven by temperature and salinity elevation. The current model predictions for *C. gibba* and *A. prismatica* were similar, rendering increased habitat suitability in the north part of the Aegean Sea, decreasing progressively towards the south part, where it is restricted in all the main enclosed bays. *Moerella donacina* presented a relatively broader distribution compared to the other species, with suitable habitats occurring in both regions. The predicted habitat suitability for *F. hyalinus* is restricted to the southern Aegean Sea and the island part of the Ionian Sea. Projecting the distributions of *C. gibba* and *A. prismatica* in future climate change scenario RCP 8.5 for the year 2100 documented similar results. SDMs for these species anticipate a significant decline of climatically suitable areas. Decline of suitable habitats was also observed for *M. donacina*; however, the effects of this scenario were not as severe as the predicted effects for *G. gibba* and *M. donacina*. An overall decrease in probability of occurrence is shown for all species except for *F. hyalinus*, which is expected to remain at relatively high levels throughout the study area and to manifest an overall significant expansion to newly suitable areas mainly in the north Aegean Sea.

The niche overlap between current and future suitability maps was different for the species used in this study. The species *C. gibba* and *A. prismatica* presented the lowest niche overlap for the similarity metric used, indicating strong alterations of habitat suitability between present and future climatic conditions (Table 2). The niche overlap for the species *F. hyalinus* was also relatively low compared to the species *M. donacina*, which recorded the highest niche overlap between present and future climate change scenario for 2100, showing some niche conservation through different climatic conditions. Overall, *C. gibba*, *A. prismatica* and *F. hyalinus* were more vulnerable to the effects of climate change as these species were unable to retain their original niche.

4. Discussion

Our initial hypothesis that the response of macrofaunal molluscs to the tested climate change scenario depends on the indicative strength of each species to its climatic space is met. The ecological group that each species was assigned to and used in marine health assessment was irrelevant under the scope of climate change. Instead, the species vulnerability to this stressor was closely linked to their autecological requirements. The SDMs employed in this study in order to assess the effects of the worst-case climate change scenario for the year 2100 showed that the habitat suitability for the bivalves *C. gibba*, *A. prismatica* and *M. donacina* is expected to decline whereas *F. hyalinus* will expand its distributional limits to newly suitable areas.

Resolving species distributions during past climatic conditions results in a better predictability of future responses. As Mediterranean fauna approached its modern temperate character, one crucial element was noticed: the migration of Atlantic species characterized by cold-loving representatives (Pérès, 1967). To this day, this state remains almost unchanged and shapes the present Mediterranean fauna. In this study, the first group of species vulnerable to the effects of climate change and global warming is the Atlantic origin species which are more abundant in the northern European seas and whose presence in the Mediterranean basin is the end result of past climatic filters. The current Mediterranean molluscan fauna is closely linked to the north-eastern Atlantic region as *C. gibba, A. prismatica* and *M. donacina* are predominantly Atlantic species that invaded the Mediterranean Sea after the Messinian Salinity Crisis which is when the first wave of faunal immigration occurred. These are the only species of this study that have been reported in both the Mediterranean basin and the North Sea during the Neogene period when the backbone of Mediterranean biota

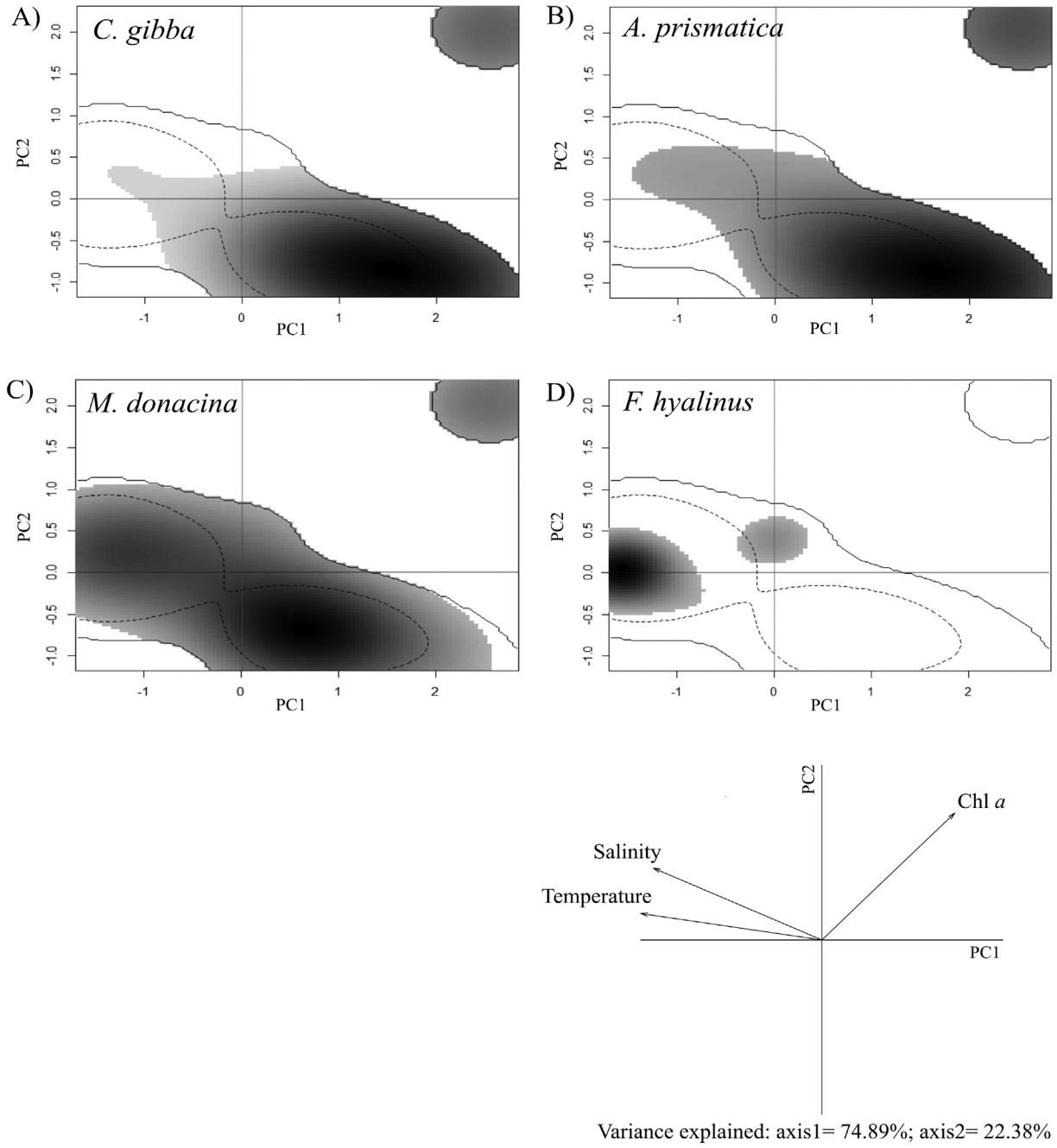


Fig. 2. Ecological niches of *C. gibba*, *A. prismatica*, *M. donacina* and *F. hyalinus* produced by the principal component analysis (PCA) method calibrating on the background climatic space of each species (A–D). The grey-black gradient shows the grid cell occupancy of the species' population records, with black representing the highest occupancy. The dashed contour line represents 50% of suitable niche space while solid contour line represents 100% of suitable niche space. The last panel shows the percentage of inertia explained by PCA axes one and two along with the contribution of the environmental predictors.

was formed (Raffi et al., 1985). Even though these species tolerated past climatic shifts they have been always linked to cold conditions. During that time the hydrographic conditions in the North Sea were described as mild summers and cold winters similar to current conditions (Raffi et al., 1985). Similar hydrographic conditions prevailed in the Mediterranean basin during the Pleistocene in addition to the severe cooling

Table 1
Relative contribution and permutation importance of each predictor to the modelling process. Mean for area under the receiver operating characteristic curve (AUC) for model evaluation.

Species	Temperature		Salinity		Chl *a*		Model evaluation
	Contr. (%)	Perm.	Contr. (%)	Perm.	Contr. (%)	Perm.	AUC
Corbula gibba	82.2	80	2.7	8	15.1	12	0.87
Abra prismatica	91.8	86.4	8	12.9	0.2	0.8	0.86
Moerella donacina	10.9	24.1	44.3	41.1	44.8	34.8	0.8
Flexopecten hyalinus	52.1	50.2	41	38.6	6.8	11.2	0.88

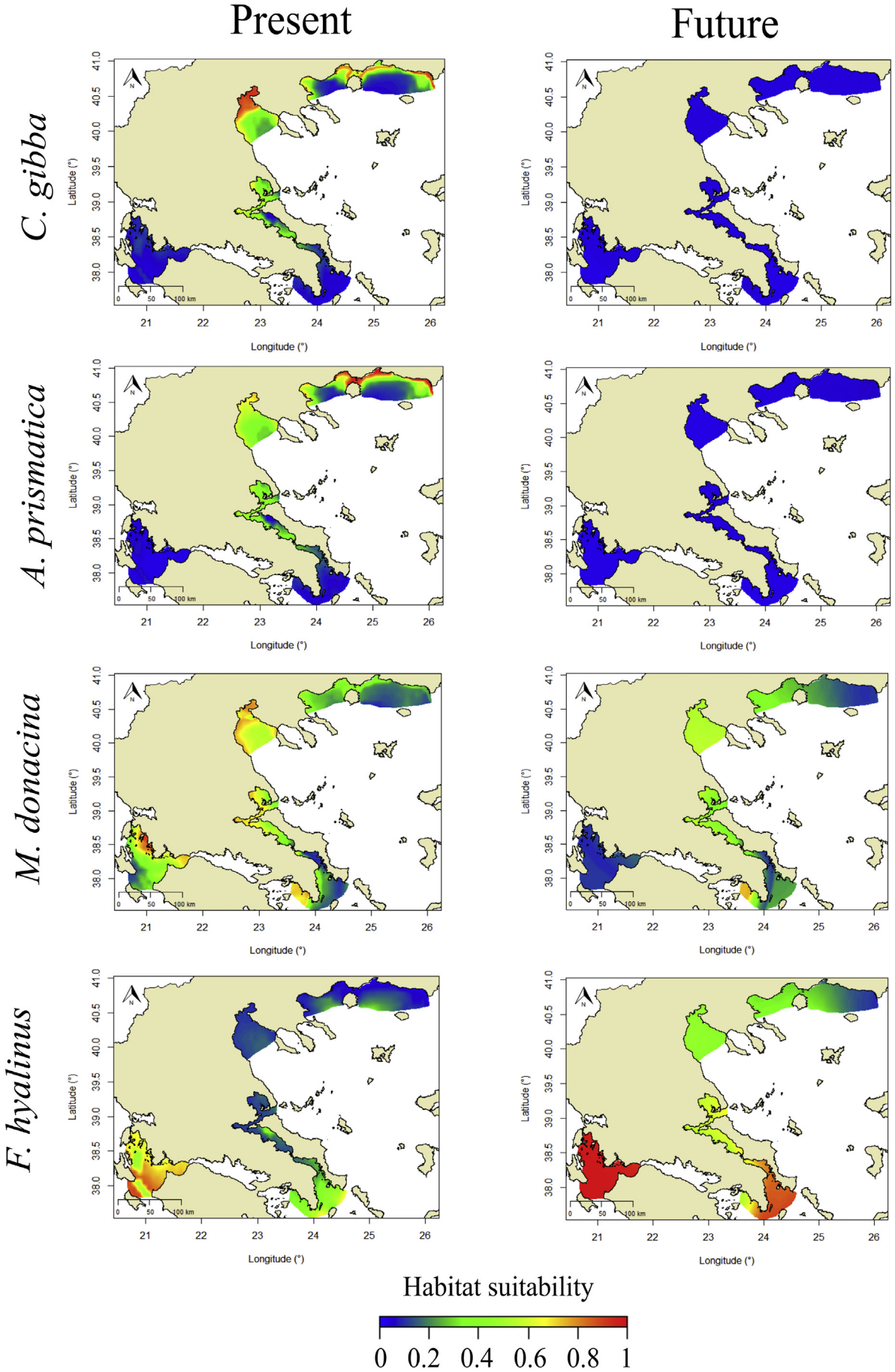


Fig. 3. Present and future (2100) habitat suitability maps generated by SDM for *C. gibba*, *A. prismatica*, *M. donacina* and *F. hyalinus*.

events during that time which eliminated other warm-water taxa. Nowadays, these species are more abundant in the North Sea, a marine area characterized by low temperatures and salinity throughout the year, an equalisation process caused by the effect of the Gulf Stream. Their current abundance in the Mediterranean Sea is lower than in the North Sea and their distribution is restricted mainly to the northern parts of the basin. In our case study, the fauna of the northern Aegean province is characterized by cold-adapted species similar to those in the north-western Mediterranean province (Bianchi, 2007; Pérès, 1967). *Corbula gibba* and *A. prismatica* rendered increased probability of occurrence in the north Aegean Sea, a marine region that is cooler, less saline and more eutrophic compared to other regions in Greece. The environmental attributes that characterize this area are caused by the dense riverine network and the Black Sea Water inflow through the Dardanelles Straits, resulting in low temperatures and salinity but increased primary productivity (Giannakourou et al., 2014; Ignatiades, 2005; Primpas and Karydis, 2011). According to the findings of this study, the increase by >3 degrees under the RCP 8.5 scenario of the minimum sea bottom temperature results in delimiting the habitat suitability, consequently eliminating the last resort for these cold-adapted species. Additionally, the ~2 degree salinity increase doesn't favour the distribution of these species either as they are tolerant to brackish conditions but not hypersaline. Similar results were observed by Weinert et al. (2016), who also documented a decrease in suitable habitats for *C. gibba* and for *Abra* and other tellinid species under climate change, addressing the importance of elevated temperature and salinity. Due to the strong association with a specific suite of climatic conditions, these species presented the least niche overlap between present and future distributions, indicating vulnerability to climate change and to niche retainment. These findings reaffirm the indicative power of *C. gibba* and *A. prismatica* to the specific hydrographic conditions described by Moraitis et al. (2018). Unlike *C. gibba* and *A. prismatica*, the tellind species *M. donacina* wasn't associated with any particular habitat type or hydrographic characteristics (not an indicator species), therefore the distributional limits of this species were much larger. Due to its broad ecological niche, this species was able to retain some of its niche space when projected to the future climate change scenario. Even though an overall spatial reduction of its essential habitat has been documented, this species was less affected by the tested climatic scenario compared to the other species of its group. This is attributed to the effects of other environmental predictors like salinity and chl *a*, which were stronger on *M. donacina* than on other species of this group. However, chl *a* in our case presented limited fluctuations between current and future climatic conditions than salinity and temperature, resulting in a significant contribution of the latter two to the modelling performance. *Moerella donacina* is classified as "sensitive" to environmental disturbance according to the most relevant benthic biotic indices used in the field of marine health assessment; however, its response to the climate change scenario tested in this case was more similar to the tolerant species that constitute the first group. This is attributed to the significant negative effect of elevated sea bottom temperature on the distribution of this species, a pattern that was also observed in the cases of *C. gibba* and *A. prismatica* (Fig. S4).

The pectinid bivalve *F. hyalinus* presented a considerably different response pattern to the other sensitive species *M. donacina*, and therefore established a group of its own. The climatic space occupied by *F. hyalinus* was defined mainly by relatively high temperature and salinity levels and described a very habitat-specific ecological niche. The strong indicative nature of *F. hyalinus* was also addressed by Moraitis et al. (2018) who characterize this species as an indicator of the same study area in terms of temperature and salinity levels. *Flexopecten hyalinus* presents very little overlap between current and future distributions, a pattern that was also observed with the other indicator species in this work *C. gibba* and *A. prismatica*. Due to its strong indicative power *F. hyalinus*, along with the other indicator species of the study, is also expected to be heavily affected by the future climatic shifts but in an exact opposite manner - by expanding its distributional limits. Predicting the response of molluscan distributions to future climatic conditions is feasible due to the extensive information of their past distributional patterns representing various climatic events (Fortunato, 2016). Unlike the other species of this study, *F. hyalinus* didn't belong to the initial Atlantic fauna that was present in both the North Sea and later in the Mediterranean basin (Raffi et al., 1985). *Flexopecten hyalinus* was characterized as a "stenothermal" species belonging to the warm-temperate or sub-tropical bivalves that colonized the Mediterranean Sea during Pliocene (Raffi et al., 1985). These warm-water taxa would spawn in the warm seasons and are therefore, closely linked to the temperatures reaching above 25 °C at that period (Monegatti and Raffi, 2001; Raffi, 1986). The current increased habitat suitability in the south Aegean Sea and the island part of the Ionian Sea is closely linked to the hydrographic conditions that define those areas. In particular, the south-central Aegean Sea is influenced by the Levantine Surface Water (LSW), a product of evaporation formed in the Levantine region (Ciappa, 2014) while the Ionian Sea is affected by the Levantine Intermediate Water (LIW), which is the net result of air-sea interactions covering all the Mediterranean basin (Menna and Poulain, 2009). The Ionian and south-central Aegean Seas are constantly fuelled by these warm and saline water masses in a way that salinity and temperature levels are maintained relatively higher than other areas, favouring the presence of *F. hyalinus* (Moraitis et al., 2018). We attribute the modelling results which predict a distributional expansion of the species by the year 2100 under elevated temperature and salinity to the newly-formed suitable area mainly in the north Aegean. Other studies have also addressed the fact that the Mediterranean Sea is progressively becoming warmer and saltier (Borghini et al., 2014; Potter and Lozier, 2004). The current mean Sea Surface Temperature (SST) in the north Aegean is ~14 °C (Bianchi, 2007; Moraitis et al., 2018) and our findings show a minimum sea bottom temperature <12 °C, which does not favour the presence of *F. hyalinus*. Additionally, the salinity levels are low in this area and prohibit the occupation by *Flexopecten* species as the gills and mantle are highly affected by hyposmotic stress in low salinity conditions (Telahigue et al., 2010).

Table 2
Niche overlap between present and future (2100) models using Schoener's *D* metric.

Species	Niche overlap
Corbula gibba	0.63
Abra prismatica	0.64
Moerella donacina	0.8
Flexopecten hyalinus	0.75

In this work, we incorporated macrofaunal species to assess the potential impact of climate change in respect of their current ecological sensitivity classification using relevant modelling methods. The species that were strongly associated with a specific suite of environmental conditions (i.e. indicators) were ideal descriptors, reflecting the effects of climate change as the impact was more profound in those species. Even though in this work we used the classification of a benthic biotic index proposed specifically for the Greek waters in order to mitigate the impact of regional differences among other biotic indices, species classified with the same ecological group still responded differently. These findings agree with Zettler et al. (2013) that such generic classification is biased when applied over large spatial scales and that indicator species are more appropriate alternatives when assessing the effects of various stressors. Current environmental disturbance thresholds for macrofaunal species are defined by benthic indices proposed for ecological status assessment. However, these indices were developed for assessing the effects of organic enrichment on the benthic compartment and consider the relative abundance of certain species as a response to organic pollution (Dauvin and Ruellet, 2007). In this study, we included chl *a* concentration, which has been previously used as a proxy for

organic sedimentary matter in the form of eutrophication in the same study area (Moraitis et al., 2018). Even though chl *a* was regarded as an important predictor in the modelling process in our case, it was not however the main driver shaping the distributional patterns under the effects of an intense climate change scenario. We attribute these results to the fact that temperature and salinity are more variant under current and future climatic conditions than any primary productivity proxy such as chl *a*. Especially for the Mediterranean basin, there is a high risk in predicting the future primary production due to the regional differences in the physico-chemical forcings, mainly in areas with river outflow and complex topography that affect primary production (Basterretxea et al., 2018). Based on the aforementioned findings, more value to temperature and salinity is automatically added in the modelling stage. Our results agree with Reiss et al. (2015) on the fact that although primary productivity measures like chl *a* are important predictors and must be included in SDM studies, the distributional barriers for marine benthic species are mostly shaped by temperature and salinity concentration. This is highly applicable when assessing the effects of climate change and global warming. The findings of this study highlight the importance of temperature and salinity as the main predictors affecting the distribution of benthic fauna when assessing the effects of climate change. Previous macrobenthic (Weinert et al., 2016) and molluscan SDM studies (Jones et al., 2013; Raybaud et al., 2014; Russell et al., 2012; Sarà et al., 2018; Saupe et al., 2014) also address the contribution of these predictors as primary distribution drivers of the benthic fauna under different climate change scenarios. Benthic biotic indices have proven to be a useful tool for detecting human induced pollution in organically enriched habitats, however, there are some limitations that need to be considered. The impact of environmental gradients like salinity and temperature may obscure the detection of macrobenthic responses and therefore the results of the biotic indices may be ambiguous (Rakocinski et al., 1997; Zettler et al., 2013). Additionally, one of the main limitations of benthic biotic indices is the assumption that all individuals of the same species would exhibit the same life strategies like feeding behaviour regardless of the environmental conditions, which, according to Maurer et al. (1999), is not the case. In our study, the incorporation of indicator species that are able to fully capture the environmental variability of the study area rendered rigorous results of climate change effects on the distribution of benthic organisms.

5. Conclusions

Our findings suggest that the more indicative a species is to its autecological requirements, the more likely it is to be affected by climate change. The current macrofaunal ecological grouping was not able to render consistent response patterns to the tested climate change scenario among the species used in this study. These results are explained by the fact that the classification process only considers the effects of human-induced organic enrichment to the benthic ecosystems and not the influence of other environmental factors like temperature and salinity, which may alter the results of those indices. Incorporating indicator species in SDM methods is a useful approach to evaluate the potential impact of climate change over large spatial scales. In this study, the macrofaunal molluscs, *C. gibba*, *A. prismatica* and *F. hyalinus* were indicative of the hydrographic conditions that characterized the Aegean and Ionian Seas and responded strongly to the tested climate change scenario. The bivalve *M. donacina*, which was not indicative of any specific climatic space, was least effected by the future environmental conditions. Past and present distributional patterns are valuable tools when predicting the response of marine species to future environmental conditions, and so molluscs are ideal candidates.

This study is built on a new perspective of using marine benthic assemblages for assessing the effects of various environmental stressors based on their ecological niche requirements. We believe that the present-state macrofaunal ecological grouping is not coherent when assessing the effects of climate change on the benthic compartment. We propose the use of species that are characterized by a very strict climatic suite in order to monitor the effects of an on-going environmental issue such as climate change.

Acknowledgements

This work was supported by the projects HYPOXIA (no 5381) and ECODISC (no 4794) both co-funded by the Greek General Secretariat for Research and Technology and the European Union under the Operational Program “Education and Lifelong Learning”. The grant from the A.G. Leventis Foundation to the first author is gratefully acknowledged. We thank the captain and the crew of the R/V PHILIA for their help during surveys. Three anonymous reviewers provided very helpful comments on the submitted manuscript. This work is dedicated by the first author to Annie and Elissa.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.02.338.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography (Cop.) 38, 541–545. https://doi.org/10.1111/ecog.01132.

Appelqvist, C., Al-Hamdani, Z.K., Jonsson, P.R., Havenhand, J.N., 2015. Climate envelope modeling and dispersal simulations show little risk of range extension of the shipworm, Teredo navalis (L.), in the Baltic Sea. PLoS One 10. https://doi.org/10.1371/journal.pone.0119217.

Basterretxea, G., Font-Muñoz, J.S., Salgado-Hernanz, P.M., Arrieta, J., Hernández-Carrasco, I., 2018. Patterns of chlorophyll interannual variability in Mediterranean biogeographical regions. Remote Sens. Environ. 215, 7–17. https://doi.org/10.1016/j.rse.2018.05.027.

Bianchi, C.N., 2007. Biodiversity issues for the forthcoming tropical Mediterranean Sea. Hydrobiologia 580, 7–21. https://doi.org/10.1007/s10750-006-0469-5.

Borghini, M., Bryden, H., Schroeder, K., Sparnocchia, S., Vetrano, A., 2014. The Mediterranean is becoming saltier. Ocean Sci. 10, 693–700. https://doi.org/10.5194/os-10-693-2014.

Borja, A., Franco, J., Pérez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Pollut. Bull. 40, 1100–1114. https://doi.org/10.1016/S0025-326X(00)00061-8.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. 21, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x.

Ciappa, A.C., 2014. The controversial path of Atlantic water in the Eastern Mediterranean. Prog. Oceanogr. 123, 74–83. https://doi.org/10.1016/j.pocean.2014.02.001.

Dauvin, J.C., Ruellet, T., 2007. Polychaete/amphipod ratio revisited. Mar. Pollut. Bull. 55, 215–224. https://doi.org/10.1016/j.marpolbul.2006.08.045.

Dauvin, J.C., Bakalem, A., Baffreau, A., Delecrin, C., Bellan, G., Lardicci, C., Balestri, E., Sardá, R., Grimes, S., 2017. The well sorted fine sand community from the western Mediterranean Sea: a resistant and resilient marine habitat under diverse human pressures. Environ. Pollut. 224, 336–351. https://doi.org/10.1016/j.envpol.2017.02.013.

de-la-Ossa-Carretero, J.A., Simboura, N., Del-Pilar-Ruso, Y., Pancucci-Papadopoulou, M.A., Giménez-Casalduero, F., Sánchez-Lizaso, J.L., 2012. A methodology for applying Taxonomic Sufficiency and benthic biotic indices in two Mediterranean areas. Ecol. Indic. 23, 232–241. https://doi.org/10.1016/j.ecolind.2012.03.029.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R.G., Hordijk, W., Salamin, N., Guisan, A., 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography (Cop.) 40, 774–787. https://doi.org/10.1111/ecog.02671.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49. https://doi.org/10.1017/S0376892997000088.

Fortunato, H., 2016. Mollusks: tools in environmental and climate research*. Am. Malacol. Bull. 33, 310–324. https://doi.org/10.4003/006.033.0208.

Galanidi, M., Kaboglu, G., Bizsel, K.C., 2016. Predicting the composition of polychaete assemblages in the Aegean coast of Turkey. Front. Mar. Sci. 3, 1–14. https://doi.org/10.3389/fmars.2016.00154.

Gama, R., Aguirre-Gutiérrez, J., Stech, M., 2017. Ecological niche comparison and molecular phylogeny segregate the invasive moss species Campylopus introflexus (Leucobryaceae, Bryophyta) from its closest relatives. Ecol. Evol. 7, 8017–8031. https://doi.org/10.1002/ece3.3301.

Giannakourou, A., Tsiola, A., Kanellopoulou, M., Magiopoulos, I., Siokou, I., Pitta, P., 2014. Temporal variability of the microbial food web (viruses to ciliates) under the influence of the Black Sea Water inflow (N. Aegean, E. Mediterranean). Mediterr. Mar. Sci. 15, 769–780. https://doi.org/10.12681/mms.1041.

Giorgi, F., 2006. Climate change hot-spots. Geophys. Res. Lett. 33, 1–4. https://doi.org/10.1029/2006GL025734.

Goldsmit, J., Archambault, P., Chust, G., Villarino, E., Liu, G., Lukovich, J.V., Barber, D.G., Howland, K.L., 2018. Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic. Biol. Invasions 20, 501–517. https://doi.org/10.1007/s10530-017-1553-7.

Gormley, K.S.G., Porter, J.S., Bell, M.C., Hull, A.D., Sanderson, W.G., 2013. Predictive habitat modelling as a tool to assess the change in distribution and extent of an OSPAR priority habitat under an increased ocean temperature scenario: consequences for marine protected area networks and management. PLoS One 8, 1–16. https://doi.org/10.1371/journal.pone.0068263.

Ignatiades, L., 2005. Scaling the trophic status of the Aegean Sea, eastern Mediterranean. J. Sea Res. 54, 51–57. https://doi.org/10.1016/j.seares.2005.02.010.

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R., Cheung, W.W.L., 2013. Applying distribution model projections for an uncertain future: the case of the Pacific oyster in UK waters. Aquat. Conserv. Mar. Freshwat. Ecosyst. 23, 710–722. https://doi.org/10.1002/aqc.2364.

Kotta, J., Möller, T., Orav-Kotta, H., Pärnoja, M., 2014. Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change. Mar. Environ. Res. 102, 88–101. https://doi.org/10.1016/j.marenvres.2014.05.002.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., Cheyne, S.M., Hearn, A.J., Ross, J., Macdonald, D.W., Mathai, J., Eaton, J., Marshall, A.J., Semiadi, G., Rustam, R., Bernard, H., Alfred, R., Samejima, H., Duckworth, J.W., Breitenmoser-Wuersten, C., Belant, J.L., Hofer, H., Wilting, A., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Distrib. 19, 1366–1379. https://doi.org/10.1111/ddi.12096.

Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T., 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol. Evol. 25, 250–260. https://doi.org/10.1016/j.tree.2009.10.009.

Macias, D.M., Garcia-Gorriz, E., Stips, A., 2015. Productivity changes in the Mediterranean Sea for the twenty-first century in response to changes in the regional atmospheric forcing. Front. Mar. Sci. 2, 1–13. https://doi.org/10.3389/fmars.2015.00079.

Marbà, N., Jordà, G., Agustí, S., Girard, C., Duarte, C.M., 2015. Footprints of climate change on Mediterranean Sea biota. Front. Mar. Sci. 2, 1–11. https://doi.org/10.3389/fmars.2015.00056.

Maurer, D., Nguyen, H., Robertson, G., Gerlinger, T., 1999. The Infaunal Trophic Index (ITI): its suitability for marine environmental monitoring. Ecol. Appl. 9, 699–713. https://doi.org/10.1890/1051-0761(1999)009[0699:TITIII]2.0.CO;2.

Menna, M., Poulain, P.M., 2009. Mediterranean subsurface circulation estimated from Argo data in 2003–2009. Ocean Sci. Discuss. 6, 2717–2753. https://doi.org/10.5194/osd-6-2717-2009.

Monegatti, P., Raffi, S., 2001. Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves. Palaeogeogr. Palaeoclimatol. Palaeoecol. 165, 171–193. https://doi.org/10.1016/S0031-0182(00)00159-0.

Moraitis, M., Papageorgiou, N., Dimitriou, P.D., Petrou, A., Karakassis, I., 2013. Effects of offshore tuna farming on benthic assemblages in the eastern Mediterranean. Aquac. Environ. Interact. 4, 41–51.

Moraitis, M.L., Tsikopoulou, I., Geropoulos, A., Dimitriou, P.D., Papageorgiou, N., Giannoulaki, M., Valavanis, V.D., Karakassis, I., 2018. Molluscan indicator species and their potential use in ecological status assessment using species distribution modeling. Mar. Environ. Res. 140, 10–17. https://doi.org/10.1016/j.marenvres.2018.05.020.

Nerlović, V., Doğan, A., Hrs-Brenko, M., 2011. Response to oxygen deficiency (depletion): bivalve assemblages as an indicator of ecosystem instability in the northern Adriatic Sea. Biologia (Bratisl) 66, 1114–1126. https://doi.org/10.2478/s11756-011-0121-3.

Pearson, T., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 16, 229–311.

Pérès, J.M., 1967. The Mediterranean benthos. Oceanogr. Mar. Biol. Annu. Rev. 5, 449–533.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/J.ECOLMODEL.2005.03.026.

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., Steenbeek, J., Danovaro, R., Christensen, V., 2017. Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. Sci. Rep. 7, 1–18. https://doi.org/10.1038/srep44491.

Potter, R.A., Lozier, M.S., 2004. On the warming and salinification of the Mediterranean outflow waters in the North Atlantic. Geophys. Res. Lett. 31, 1–4. https://doi.org/10.1029/2003GL018161.

Primpas, I., Karydis, M., 2011. Scaling the trophic index (TRIX) in oligotrophic marine environments. Environ. Monit. Assess. 178. https://doi.org/10.1007/s10661-010-1687-x.

R Development Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.r-project.org/ (Version: 3.4.3).

Raffi, S., 1986. The significance of marine boreal molluscs in the Early Pleistocene faunas of the Mediterranean area. Palaeogeogr. Palaeoclimatol. Palaeoecol. 52, 267–289. https://doi.org/10.1016/0031-0182(86)90051-9.

Raffi, S., Stanley, S.M., Marasti, R., 1985. Biogeographic patterns and Plio-Pleistocene extinction of Bivalvia in the Mediterranean and southern North Sea. Paleobiology 11, 368–388. https://doi.org/10.1017/S0094837300011684.

Rakocinski, C.F., Brown, S.S., Gaston, G.R., Heard, R.W., Walker, W., Summers, J.K., 1997. Macrobenthic responses to natural and contaminant-related gradients in Northern Gulf of Mexico Estuaries Published by: Ecological Society of America. Stable URL:. http://www.jstor.org/stable/2641214 Ecol. Appl. 7, 1278–1298. https://doi.org/10.1890/1051-0761(1997)007[1278:MRTNAC]2.0.CO;2.

Raybaud, V., Beaugrand, G., Dewarumez, J.M., Luczak, C., 2014. Climate-induced range shifts of the American jackknife clam Ensis directus in Europe. Biol. Invasions 17, 725–741. https://doi.org/10.1007/s10530-014-0764-4.

Reiss, H., Birchenough, S., Borja, A., Buhl-mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A.M., Valle, M., Van Hoey, G., Zettler, M.L., Degraer, S., 2015. Benthos distribution modelling and its relevance for marine ecosystem management. ICES J. Mar. Sci. 72, 297–315.

Rödder, D., Engler, J.O., 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Glob. Ecol. Biogeogr. 20, 915–927. https://doi.org/10.1111/j.1466-8238.2011.00659.x.

Rosenberg, R., Blomqvist, M., C Nilsson, H., Cederwall, H., Dimming, A., 2004. Marine quality assessment by use of benthic species-abundance distributions: a proposed new protocol within the European Union Water Framework Directive. Mar. Pollut. Bull. 49, 728–739. https://doi.org/10.1016/j.marpolbul.2004.05.013.

Russell, B.D., Connell, S.D., Mellin, C., Brook, B.W., Burnell, O.W., Fordham, D.A., 2012. Predicting the distribution of commercially important invertebrate stocks under future climate. PLoS One 7. https://doi.org/10.1371/journal.pone.0046554.

Saeedi, H., Basher, Z., Costello, M.J., 2017. Modelling present and future global distributions of razor clams (Bivalvia: Solenidae). Helgol. Mar. Res. 70. https://doi.org/10.1186/s10152-016-0477-4.

Sánchez-Moyano, J.E., García-Asencio, I., Donázar-Aramendía, I., Miró, J.M., Megina, C., García-Gómez, J.C., 2017. BENFES, a new biotic index for assessing ecological status of soft-bottom communities. Towards a lower taxonomic complexity, greater reliability and less effort. Mar. Environ. Res. 132, 41–50. https://doi.org/10.1016/j.marenvres.2017.10.014.

Sarà, G., Porporato, E.M.D., Mangano, M.C., Mieszkowska, N., 2018. Multiple stressors facilitate the spread of a non-indigenous bivalve in the Mediterranean Sea. J. Biogeogr. 45, 1090–1103. https://doi.org/10.1111/jbi.13184.

Saupe, E.E., Hendricks, J.R., Townsend Peterson, A., Lieberman, B.S., 2014. Climate change and marine molluscs of the western North Atlantic: future prospects and perils. J. Biogeogr. 41, 1352–1366. https://doi.org/10.1111/jbi.12289.

Simboura, N., Zenetos, A., 2002. Benthic indicators to use in ecological quality classification of Mediterranean soft bottom marine ecosystems, including a new Biotic Index. Mediterr. Mar. Sci. 3, 77–111. https://doi.org/10.12681/mms.249.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, Nick, Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., Mcmanus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57, 573. https://doi.org/10.1641/B570707.

Telahigue, K., Rabeh, I., Chetoui, I., Romdhane, M.S., EL Cafsi, M., 2010. Effects of decreasing salinity on total lipids and fatty acids of mantle and gills in the bivalve *Flexopecten glaber* (Linnaeus, 1758) under starvation. Cah. Biol. Mar. 51, 301–309.

Townhill, B., Pinnegar, J., Tinker, J., Jones, M., Simpson, S., Stebbing, P., Dye, S., 2017. Non-native marine species in north-west Europe: developing an approach to assess future spread using regional downscaled climate projections. Aquat. Conserv. Mar. Freshwat. Ecosyst. https://doi.org/10.1002/aqc.2764.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob. Ecol. Biogeogr. 21, 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Clim. Chang. 109, 5–31. https://doi.org/10.1007/s10584-011-0148-z.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution (N. Y) 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography (Cop.) 33, 607–611. https://doi.org/10.1111/j.1600-0587.2009.06142.x.

Weinert, M., Mathis, M., Kröncke, I., Neumann, H., Pohlmann, T., Reiss, H., 2016. Modelling climate change effects on benthos: distributional shifts in the North Sea from 2001 to 2099. Estuar. Coast. Shelf Sci. 175, 157–168. https://doi.org/10.1016/j.ecss.2016.03.024.

WoRMS Editorial Board, 2018. World Register of Marine Species. https://doi.org/10.14284/170.

Zettler, M.L., Proffitt, C.E., Darr, A., Degraer, S., Devriese, L., Greathead, C., Kotta, J., Magni, P., Martin, G., Reiss, H., Speybroeck, J., Tagliapietra, D., Van Hoey, G., Ysebaert, T., 2013. On the myths of Indicator species: issues and further consideration in the use of static concepts for ecological applications. PLoS One 8. https://doi.org/10.1371/journal.pone.0078219.